Primary Productivity in a Hawaiian Fishpond and Its Relationship to Selected Environmental Factors[1]

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ABSTRACT: Community, microbenthic, and planktonic metabolic rates were measured in a Hawaiian fishpond from June 1966 through June 1967. Incident and penetrating light intensity, dissolved phosphate, nitrate and nitrite, and silicate, temperature, salinity, and pH were measured concurrently. Primary productivity and respiration were greatest in the fall and spring. Primary productivity was most frequently limited by light intensity because of the turbidity of the pond water. Dissolved inorganic nutrients did not appear to be limiting. Community respiration exceeded gross primary productivity by 212 g C/m^2 yr. Organic matter was probably imported from the surrounding mangrove swamp.

THE MULLET *Mugil cephalus* and the milkfish *Chanos chanos* are raised commercially in marine and brackish-water fishponds throughout the world (D'Ancona, 1954), but their ecology is little known. Hiatt (1944) observed that mullet and milkfish in Hawaiian fishponds feed primarily on microbenthic algae and organic detritus. This agrees with observations in the Philippines (Herre and Mendoza, 1929; Adams et al., 1932) and elsewhere (Ghazzawi, 1933). Rabanal et al. (1951) estimated the production of benthic algae in Philippine fishponds and observed greatest growth during the rainy season.

The primary productivity of other shallow inshore habitats has been studied (e.g., Odum and Hoskin, 1958; Pomeroy, 1959, 1960; Grøntved, 1960), but few investigators have evaluated the relative importance of the benthic and planktonic components. Data on the primary productivity of microbenthic algae are especially lacking.

The objectives of this investigation were to measure the primary productivity in a Hawaiian fishpond and to evaluate it with respect to solar radiation, dissolved inorganic nutrients, and temperature. This should (i) provide information on the relationship between primary productivity and the physical environment *in situ*, (ii) indicate the relative importance of benthic and planktonic primary productivity, and (iii) give an insight into possible methods of increasing the quantity of food available to pond-reared mullet and milkfish.

DESCRIPTION OF THE FISHPOND ECOSYSTEM

The experimental pond (Fig. 1), located on the south shore of Molokai, has an area of 75,000 m^2 and a basalt wall 810 meters long forming a semicircular enclosure over the reef flat. Water passes through the wall with the rise and fall of the tide, but the fish are retained within the enclosure. The mean depth of the pond ranges from 10 to 100 cm depending on the tide. The pond bottom consists of 10 to 30 cm of black to brown silt overlying a dead coral substratum. An algal mat, dominated by pennate diatoms and blue-green algae, covers the pond bottom. Macrobenthic algae are sparse. A mangrove swamp bordering the pond acts as a windbreak and provides an external source of organic matter.

Philippine fishponds, in contrast to Hawaiian fishponds, vary in size and depth depending on whether fry, fingerlings, or juveniles are to be reared in them. By controlling the depth of the

[1] This investigation was supported by the Oceanic Institute through a grant to the University of Hawaii and was a part of a thesis submitted to the Graduate Division of the University of Hawaii in partial fulfillment of the requirements for the degree of Master of Science. Manuscript received April 4, 1968.

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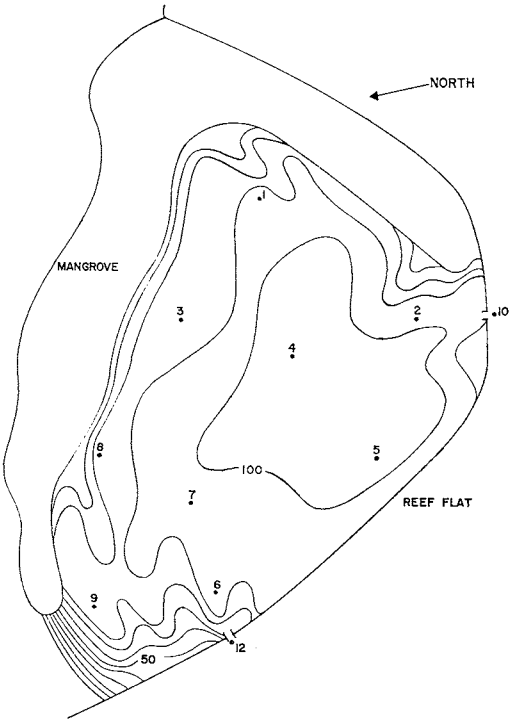

FIG. 1. Location of stations and bathymetry of the experimental pond; contour interval 10 cm.

ponds, different species of microbenthic algae are encouraged to grow, and competitors and predators are effectively excluded (Frey, 1947). Predators, such as barracuda and lizard fish, and competitors, such as gobies and sail-fins, are able to enter and leave Hawaiian ponds almost at will.

MATERIALS AND METHODS

Environmental Factors

The data were collected at monthly intervals from June 1966 through June 1967. The colorimetric methods used for the determination of reactive phosphorus and silicon are described by Strickland and Parsons (1965), and that for nitrate, nitrite nitrogen by Strickland and Parsons (1960). Surface water temperatures were measured at 3-hour intervals from sunrise to sunset.

A Schueler submarine photometer was used to estimate incident solar radiation and radiation penetrating to the pond bottom. The deck and submarine units were placed on platforms located at the water's edge and on the pond bottom, respectively. Measurements of incident and pentrating light intensities were made at half-hour intervals from sunrise to sunset. Total daily radiation (langlies/day) was determined by plotting these values (langlies/min) against time and measuring the area under the curve with a planimeter.

The Schueler photometer employs Weston Photronic cells. These cells respond to wavelengths between 300 mμ and 750 mμ, with a maximum near 550 mμ (Strickland, 1958). This spectral range corresponds approximately to the range of photosynthetically active wavelengths (Haxo and Blinks, 1950).

The Weston cells were calibrated against an Eppley pyrheliometer on a bright, cloudless day. The output of the cells was assumed to be proportional to the output of the pyrheliometer (Strickland, 1958). The pyrheliometer is equally sensitive to all wavelengths between 380 mμ and 2900 mμ and measures about twice as much light energy as do the Weston cells on the average. Therefore, to relate light intensity to photosynthetic activity, pyrheliometer readings were divided by 2 (Edmondson, 1956; Talling, 1957; Strickland, 1958).

Primary Productivity

Two approaches based on changes in dissolved oxygen were used to measure primary productivity and respiration. The microbenthic and planktonic components of community metabolism were estimated separately by a closed system approach in which samples were enclosed in containers and incubated *in situ*. The primary productivity and respiration of the fishpond community as a whole was estimated by an open system approach similar to the "*in situ*" method (Gilmartin, 1964) and the "free water" method (Odum and Hoskin, 1958). Dissolved oxygen was measured by the Winkler technique (Strickland and Parsons, 1965). Water samples were fixed immediately upon collection and titrated within ½ hour of collection.

Microbenthic algal productivity was estimated by a method similar to the bell jar technique (Odum, 1957; Odum and Hoskin, 1958; Pomeroy, 1960). Plexiglas boxes open at one

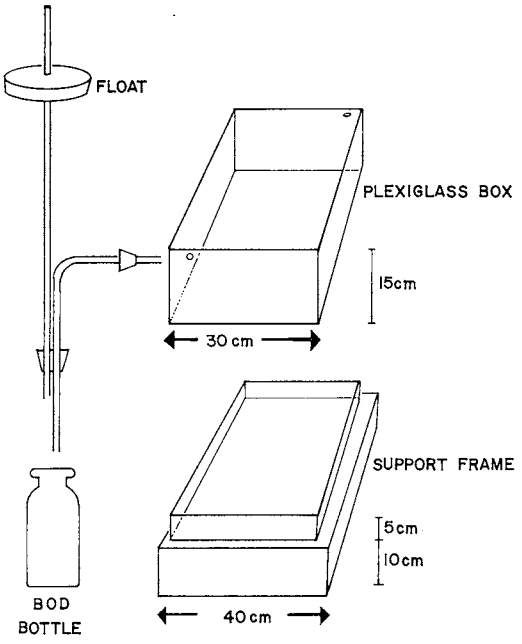

FIG. 2. Apparatus for measuring microbenthic primary productivity and respiration by the closed system approach.

end were placed over fiberglassed wooden frames (Fig. 2), open top and bottom, and permanently fixed in the soft substratum of the pond bottom. Water samples for oxygen analysis were drawn from the boxes within ±15 minutes of sunset, sunrise, and again sunset. Any silt that had collected on the tops of the boxes was periodically removed throughout the day. The plexiglas boxes were taken from the pond at the end of the 24-hour cycle. Considering the surface area provided by the silt substratum of the pond and the exceptionally high rates of bacterial respiration usually observed in similar environments (ZoBell and Feltham, 1942), any bacterial respiration due to the presence of the plexiglas boxes per se should be insignificant. Phytoplankton productivity in the boxes was assumed to be negligible because of the rapid attenuation of light intensity with depth in the pond. A photosynthetic quotient of 1.2 and a respiratory quotient of 1.0 (Ryther, 1956*a*; Strickland, 1960) were used in calculating primary productivity and respiration.

Phytoplankton productivity was estimated by the standard BOD bottle technique (Gaarder and Gran, 1927). Two light bottles and one dark bottle were filled with surface water at three stations and suspended at the surface. The incubation periods were 24 hours for the dark bottles and from sunrise to sunset for the light bottles. The longer incubation period was needed for the dark bottles because of low respiratory rates, although it was recognized that this would increase the error due to bacterial respiration (Strickland, 1960). Since adequate correction factors are not available and planktonic respiration was small compared to the respiration of the entire fishpond community, no attempt was made to correct for this error. Phytoplankton productivity per unit area was calculated, assuming that productivity per unit volume was a linear function of light intensity which decreased exponentially with depth. Productivity was directly proportional to intensities below 550 ly/day and inversely proportional to intensities above 550 ly/day (Fig. 7).

The primary productivity and respiration of the entire fishpond community was measured directly by an oxygen budget method based on diel oxygen changes *in situ*. The concentration of dissolved oxygen in the pond water and in the water entering or leaving the pond was determined at sunset and at 3-hour intervals from sunrise to sunset the following day. The oxygen changes observed over each time interval ($\triangle Q_o$) were assumed to result from the interaction of three factors: (1) advective processes (Q_a), (2) diffusion across the air-sea interface (Q_e), and (3) biological activity (Q_b). Thus

$$\triangle Q_o = \triangle Q_a + \triangle Q_e + \triangle Q_b$$
$$\text{and } \triangle Q_b = \triangle Q_o - \triangle Q_a - \triangle Q_e.$$

The change in dissolved oxygen due to advection was found by measuring changes in pond volume over each time interval and multiplying this by the mean oxygen content of the water entering or leaving the pond during that interval. Changes in oxygen caused by diffusion across the sea surface were calculated by the method of Redfield (1948). Redfield's summer exchange coefficient (4.72×10^3 mg O_2/m^2 hr atm) was used, corrected for the oxygen saturation values reported by Truesdale et al. (1955).

TABLE 1

COMMUNITY METABOLISM (g C/m² 24 hr) FROM 23 JUNE 1966 TO 8 JUNE 1967 IN THE EXPERIMENTAL POND

Microbenthic (B) and planktonic (P) primary productivity were measured by the closed system approach, and community (C) metabolism by the open system approach. Annual values (g C/m²) are given at the bottom of the table.

	GROSS PRODUCTIVITY		RESPIRATION			NET PRODUCTIVITY		
DATE	B	P	C	B	P	C	B	P
6/23	0.28	0.16	1.10	0.34	0.06	−0.38	−0.06	+0.10
7/27	0.28	0.25	1.34	0.34	0.10	−0.43	−0.06	+0.15
8/23	0.48	0.38	1.73	0.59	0.19	−0.30	−0.11	+0.19
9/25	0.50	0.22	2.61	0.60	0.08	−0.71	−0.10	+0.14
10/23	0.48	0.24	1.95	0.60	0.08	−0.88	−0.12	+0.16
11/27	0.34	0.02	1.18	0.43	0.04	−0.48	−0.09	−0.02
12/20	0.45	0.05	1.25	0.55	0.03	−0.60	−0.10	+0.02
1/19	0.37	0.09	1.05	0.44	0.06	−0.36	−0.07	+0.03
2/19	0.35	0.08	1.79	0.41	0.04	−0.83	−0.06	+0.04
3/19	0.58	0.10	2.59	0.83	0.03	−1.08	−0.25	+0.07
4/16	0.83	0.12	2.91	0.93	0.07	−0.17	−0.10	+0.05
5/14	0.80	0.12	2.67	0.90	0.06	−0.32	−0.10	+0.06
6/8	0.44	0.15	2.20	0.62	0.09	−1.01	−0.18	+0.06
Annual	173	49	657	204	25	−212	−31	+24

RESULTS AND DISCUSSION

Primary Productivity of the Pond Ecosystem

Mean values for primary productivity and respiration are given in Table 1. Measurements of net productivity included the respiratory consumption of oxygen by animals and bacteria as well as by primary producers. Thus microbenthic, planktonic, and community net productivity represent the amount of oxygen produced in excess of the respiratory demands of each system.

Planktonic net productivity was predominantly positive during the investigation, but community and microbenthic net productivity were consistently negative. Community respiration exceeded primary productivity by 212 g C/m² yr. Therefore, the experimental pond was heterotrophic (Odum, 1956*a*), and imported organic matter, probably in the form of mangrove leaves and other detritus carried into the pond by runoff and tidal action, constituted an important source of energy for the fishpond community.

Annual gross primary productivity of the pond community measured by the closed system approach was 222 g C/m². Of this, plankton producers contributed 22 per cent and microbenthic producers 78 per cent. There is evidence that these estimates of gross primary productivity were low and that the value of 445 g C/m² yr (Table 2) calculated by the open system approach is more realistic. However, the relative importance of planktonic and benthic productivity probably was correct (Pomeroy, 1960). This is supported by the significance ($p = 0.01$) of the correlation ($r = 0.890$) between productivity as measured

TABLE 2

BALANCE SHEET FOR THE POND COMMUNITY

(Organic imports were calculated by subtracting gross productivity from community respiration. All values expressed as g C/m² yr.)

Gross productivity		
Benthic	347	
Planktonic	98	
Respiration		
Benthic		378
Planktonic		74
Other		205
Organic imports	212	
Total	657	657

by the open system approach and by the closed system approach.

Annual community respiration, measured by the open system approach, was 657 g C/m^2. Measured by the closed system approach, benthic and planktonic respiration combined was 229 g C/m^2 yr. The remaining 428 g C/m^2 yr may represent the respiration of larger organisms in the pond not contained in the closed systems, but this seems high. It is likely that the absence of turbulent flow in the plexiglas boxes and BOD bottles limited metabolic rates (Odum, 1956*b*, 1957). It has been shown (Munk and Riley, 1952; Whitford, 1960; Whitford and Schumacher, 1964) that flow past an organism increases the exchange rate of materials between the organism and its environment and promotes metabolic processes that are (i) limited by the availability of dissolved gases and nutrients, and (ii) inhibited by an accumulation of metabolic wastes.

The annual balance sheet for the pond community is given in Table 2. The primary productivity of the ecosystem provided 68 per cent and organic imports 32 per cent of the energy requirements of the fishpond community. Microbenthic producers were the most important source of organic material in the fishpond, accounting for 53 per cent of the annual total.

Primary Productivity in Relation to the Environment

Gross primary productivity in the fishpond had two peaks during the year, one in late summer and early fall and the other in the spring (Fig. 3). The smaller peak in August was caused by an increase in phytoplankton productivity, while the spring maximum was caused by an increase in microbenthic productivity.

Dissolved nutrient salts limit primary productivity by the rate at which they are made available rather than by their concentrations (Harvey, 1942; Ketchum et al., 1958; Ryther and Guillard, 1959), which represent a balance between the rates of supply and consumption. Thus, if seasonal variations in the concentrations of dissolved inorganic nutrients are to be reflected by changes in primary productivity, fluctuations in the rate of autotrophic consumption must be greater in amplitude than fluctuations in the rate of replenishment.

Monthly fluctuations in dissolved inorganic nutrients appeared to be unrelated (Fig. 4). Dissolved PO_4-P remained relatively constant at about 0.6 µg-at/1 while dissolved NO_3, NO_2-N was high during the summer and spring and low during the winter. The ratio of nitrogen to phosphorus ranged from 5 to 35 with a mean of 16. Dissolved SiO_4-Si exhibited no distinct pattern but fluctuated by more than tenfold during the year.

Changes in the primary productivity of the pond community were rarely related to changes in the concentrations of these nutrients. Since PO_4-P remained relatively constant and was usually above the limiting concentration of 0.5 µg-at/1 (Ketchum, 1939), it is doubtful that it ever was limiting. Both nitrogen and silicon

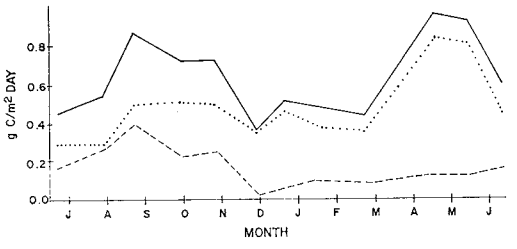

FIG. 3. Gross primary productivity in the experimental pond from 23 June 1966 to 8 June 1967: planktonic (- - - -), microbenthic (. . . .), and total (——) productivity.

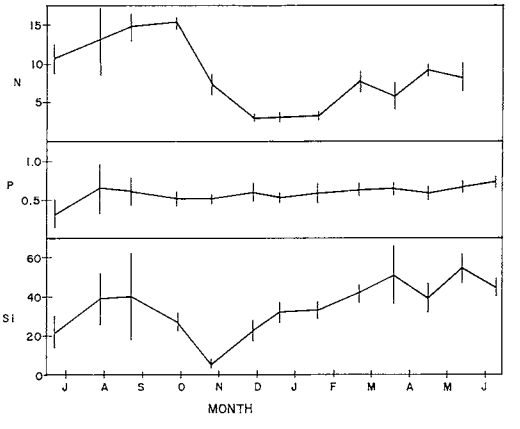

FIG. 4. Mean concentration (µg-at/1) of dissolved NO_3, NO_2-N (N), PO_4-P (P), and SiO_2-Si (Si) with 95% confidence intervals from 23 June 1966 to 8 June 1967.

may have been limiting during the late fall and winter because (i) productivity declined sharply following a drop in dissolved silicon to 5 μg-at/1 in October; (ii) productivity remained low during the winter when dissolved nitrogen was reduced to about 3 μg-at/1; and (iii) productivity began to increase in February following a sharp rise in nitrogen concentration. Strickland (1965) gives 2–4 μg-at SiO_4-Si/1 and 4 μg-at NO_3-N/1 as being limiting to diatom growth. Perhaps nitrogen was limiting during the winter, and the rise in nitrogen content in February set the stage for the subsequent spring increase in productivity.

Incident radiation (Fig. 5) varied from 360 ly/day in November to 692 ly/day in June, 1967. Radiation penetrating to the pond bottom varied from 79 ly/day in July to 328 ly/day in April. The percentage of incident light penetrating to the pond bottom ranged from 10 per cent to 50 per cent and was primarily a function of turbidity and water depth. The intensity of turbulent mixing, a function of water depth and wind stress, controlled the turbidity of the pond water.

The rate of photosynthesis is proportional to light at low intensities. As light intensity increases, a saturating intensity is reached beyond which increased illumination may inhibit photosynthesis. Ryther (1956*b*) observed that the photosynthetic rates of four diatom species were light-saturated at about 0.07 ly/min and were light-inhibited above 0.15 ly/min. Similar results have been found for other plankton diatoms (Talling, 1957; Curl and McLeod, 1961). However, McAllister et al. (1964) found that the maximum photosynthetic rates of four marine phytoplankton species grown at optimal temperatures occurred at about 0.1 ly/min and that little inhibition occurred when the intensity was increased to as high as 0.4 ly/min. Taylor and Palmer (1963) observed that the optimum light intensity for a littoral diatom community was 0.2 ly/min and that there was only 10 per cent inhibition at 1.2 ly/min.

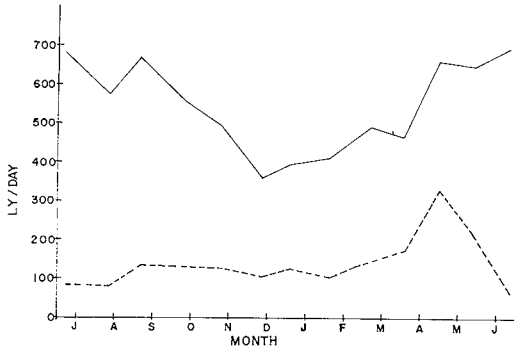

FIG. 5. Incident light intensity (——) and light intensity penetrating to the pond bottom (- - - -) from 23 June 1966 to 8 June 1967.

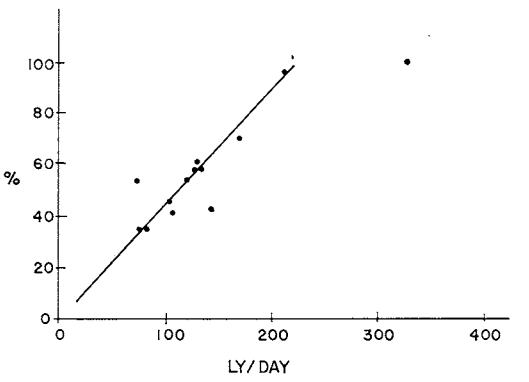

FIG. 6. Relative microbenthic productivity (% of maximum measured value) as a function of penetrating light intensity.

Microbenthic gross productivity per day in the experimental fishpond was light-limited throughout the investigation (Fig. 6), but optimum light intensities may have been reached between 200 and 300 ly/day (0.3–0.4 ly/min). Penetrating intensities above 200 ly/day were observed only twice (Fig. 5), 16 April and 14 May, and coincided with calm periods. Therefore, because it controls penetrating light energy, turbidity was an important factor limiting microbenthic productivity in the fishpond.

Surface phytoplankton productivity was light-inhibited during the spring and summer when incident light intensities exceeded 600 ly/day and was light-limited during the winter when incident light intensities fell below 500 ly/day (Fig. 7). Both microbenthic and planktonic productivity were light-limited during the winter, but surface planktonic productivity was light-inhibited during the spring when microbenthic productivity reached its maximum.

The effect of varying light intensities on primary productivity is greatly modified by

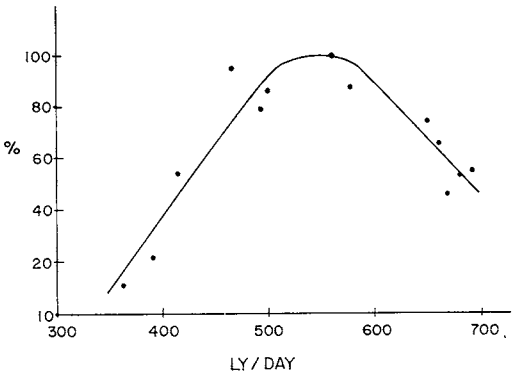

FIG. 7. Relative surface phytoplankton productivity per unit volume (% of maximum measured value) as a function of incident light intensity.

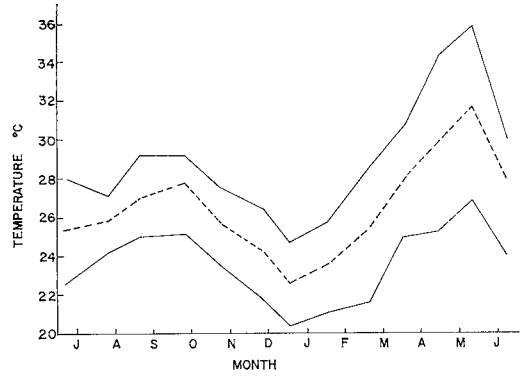

FIG. 8. Diurnal mean water temperature (- - - -) and diurnal range of mean pond temperature (——) from 23 June 1966 to 8 June 1967.

temperature (Sorokin, 1958; Curl and McLeod, 1961), and the two should be considered simultaneously. Mean daily temperatures of the pond water varied seasonally from 22.6°C in December to 31.7°C in May (Fig. 8), and the diurnal cycle of mean pond temperatures varied in amplitude from 3°C to 9°C. Microbenthic productivity was significantly correlated ($p = 0.01$) with both mean daily water temperature ($r = 0.795$) and penetrating radiation ($r = 0.883$). The multiple correlation for the combined effect of both variables ($R = 0.933$) is highly significant ($p < 0.01$). Thus, although light was the dominant factor, the interaction between variations in light and temperature determined the monthly variation in microbenthic primary productivity. Similar results have been found for both freshwater (Round, 1953) and marine (Smyth, 1955; Pomeroy, 1959) benthic diatoms.

Undoubtedly the measured levels of primary productivity in the experimental fishpond were the result of the interaction of light intensity, temperature, and nutrients, as well as many variables that were not investigated, such as light quality, grazing rate, micronutrients, dissolved organics, and growth factors. But during the period of study the quantity of available light was the predominant limiting factor because of the turbidity of the pond water. Nutrient supply was of minor importance and under present conditions will not be of any great significance unless turbidity is eliminated as a limiting factor.

Due to the large number of food chains in the pond involving microbenthic algae and mullet that were terminated by animals other than mullet (e.g., sail-fins, gobies, lizard fish, and barracuda) and the possibility that the mullet in the fishpond were subsisting primarily on organic detritus, no realistic estimate of annual mullet productivity can be made from the observed annual primary productivity. It is clear, however, that the yield of mullet from the pond will be higher if the turbidity of the pond water is eliminated, thereby increasing the amount of light energy available to the microbenthic algae.

SUMMARY

Community, microbenthic, and planktonic primary productivity were measured in a Hawaiian fishpond using two approaches based on changes in dissolved oxygen. A closed system approach was used to estimate microbenthic and planktonic productivity, and an open system approach was used to estimate the total productivity of the pond ecosystem.

Gross primary productivity, which was greatest in the fall and spring, was underestimated by the closed system approach. The annual productivity of the fishpond was 445 g C/m^2, of which 78 per cent was microbenthic and 22 per cent planktonic. Community respiration exceeded gross productivity by 212 g C/m^2 yr.

Microbenthic primary productivity was light-limited during the entire investigation. Surface phytoplankton productivity was limited by in-

cident light intensities below about 500 ly/day and inhibited above 600 ly/day. Dissolved inorganic nutrients did not appear to be limiting during the investigation. Turbidity, through its control of penetrating light energy, was the most important factor limiting primary productivity in the fishpond.

LITERATURE CITED

ADAMS, W., H. R. MONTALBAN, and C. MARTIN. 1932. Cultivation of bangos in the Philippines. Philippine Journal of Science, vol. 47, pp. 1–38.

CURL, H., and G. C. MCLEOD. 1961. The physiological ecology of a marine diatom, *Skeletonema costatum* (Grev.) Cleve. Journal of Marine Research, vol. 19, no. 2, pp. 70–88.

D'ANCONA, U. 1954. Fishing and fish culture in brackish-water lagoons. Fisheries Bulletin F.A.O., vol. 7, no. 4, pp. 147–172.

EDMONDSON, W. T. 1956. The relation of photosynthesis by phytoplankton to light in lakes. Ecology, vol. 37, no. 1, pp. 161–174.

FREY, D. G. 1947. The pond fisheries of the Philippines. Journal of Marine Research, vol. 6, pp. 247–258.

GAARDER, T., and H. H. GRAN. 1927. Investigations of the production of plankton in the Oslo Fjord. Rapport et procès-verbaux des réunions. Conseil permanent international pour l'exploration de la mer, vol. 42, pp. 1–31.

GHAZZAWI, F. M. 1933. The pharynx and intestinal tract of the Egyptian mullets—*Mugil cephalus* and *Mugil capito*. Part I. On the food of mullet from Egyptian waters. Fishery Research Directorate, Cairo, Notes and Memoirs, no. 5, 18 pp.

GILMARTIN, M. 1964. The primary productivity of a British Columbia fjord. Journal of the Fisheries Research Board of Canada, vol. 21, no. 3, pp. 505–538.

GRØNTVED, J. 1960. On the productivity of microbenthos and phytoplankton in some Danish fjords. Meddelelser Danmarks Fiskieri- og Havundersogelser, NS 3, pp. 55–92.

HARVEY, H. W. 1942. Production of life in the sea. Biological Reviews, vol. 17, pp. 221–246.

HAXO, F. T., and L. R. BLINKS. 1950. Photosynthesis action spectra of marine algae. Journal of General Physiology, vol. 33, pp. 389–422.

HERRE, A. W., and J. MENDOZA. 1929. Bangos culture in the Philippine Islands. Philippine Journal of Science, vol. 38, pp. 451–505.

HIATT, R. W. 1944. Food chains and food cycles in Hawaiian fishponds, Parts 1 and 2. Transactions of the American Fisheries Society, vol. 74, pp. 250–280.

KETCHUM, B. H. 1939. The absorption of phosphate and nitrate by illuminated cultures of *Nitzschia closterium*. American Journal of Botany, vol. 26, pp. 399–407.

KETCHUM, B. H., J. H. RYTHER, C. S. YENTSCH, and N. CORWIN. 1958. Productivity in relation to nutrients. Rapport et procès-verbaux des réunions. Conseil permanent international pour l'exploration de la mer, vol. 144, pp. 132–140.

MCALLISTER, C. D., N. SHAH, and J. D. H. STRICKLAND. 1964. Marine phytoplankton photosynthesis as a function of light intensity: A comparison of methods. Journal of the Fisheries Research Board of Canada, vol. 21, no. 1, pp. 151–181.

MUNK, W. H., and G. A. RILEY. 1952. Absorption of nutrients by aquatic plants. Journal of Marine Research, vol. 11, pp. 215–240.

ODUM, H. T. 1956*a*. Efficiencies, size of organisms, and community structure. Ecology, vol. 37, no. 3, pp. 592–597.

——— 1956*b*. Primary production in flowing waters. Limnology and Oceanography, vol. 1, no. 2, pp. 102–117.

——— 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs, vol. 27, pp. 55–112.

ODUM, H. T., and C. M. HOSKIN. 1958. Comparative studies on the metabolism of marine waters. Publications of the Institute of Marine Science, University of Texas, vol. 5, pp. 16–46.

POMEROY, L. R. 1959. Algal productivity in salt marshes of Georgia. Limnology and Oceanography, vol. 4, no. 1, pp. 386–397.

——— 1960. Primary productivity of Boca Ciega Bay, Florida. Bulletin of Marine Science of the Gulf and Caribbean, vol. 10, no. 1, pp. 1–10.

RABANAL, H. R., R. S. ESGUERRA, J. V. LOPEZ, A. M. ALDANA, V. R. RAMOS, and S. S. FELIX. 1951. The rate of algae (lumut) production in the Dagat-Dagatan salt-water fishery experimental station fishponds. Philippine Journal of Fisheries, vol. 1, no. 2, pp. 155–169.

REDFIELD, A. C. 1948. The exchange of oxygen across the sea surface. Journal of Marine Research, vol. 7, pp. 347–361.

ROUND, F. E. 1953. An investigation of two benthic algal communities in Malham Tarn, Yorkshire. Journal of Ecology, vol. 41, pp. 174–197.

RYTHER, J. H. 1956*a*. The measurement of primary production. Limnology and Oceanography, vol. 1, no. 2, pp. 72–84.

——— 1956*b*. Photosynthesis in the ocean as a function of light intensity. Limnology and Oceanography, vol. 1, no. 1, pp. 61–70.

RYTHER, J. H., and R. R. L. GUILLARD. 1959. Enrichment experiments as a means of studying nutrients limiting to phytoplankton production. Deep Sea Research, vol. 6, pp. 65–69.

SMYTH, J. C. 1955. A study of the benthic diatoms of Loch Sween. Journal of Ecology, vol. 43, pp. 149–171.

SOROKIN, C. 1958. The effect on the past history of cells of *Chlorella* on their photosynthetic capacity. Physiologia Plantarum, vol. 11, pp. 275–283.

STRICKLAND, J. D. H. 1958. Solar radiation penetrating the ocean. Journal of the Fisheries Research Board of Canada, vol. 15, no. 3, pp. 453–493.

——— 1960. Measuring the production of marine phytoplankton. Bulletin of the Fisheries Research Board of Canada, no. 122, 172 pp.

——— 1965. Production of organic matter in the primary stages of the marine food chain, pp. 478–610. In: J. P. Riley and G. Skirrow, eds., Chemical Oceanography. New York, Academic Press.

STRICKLAND, J. D. H., and T. R. Parsons. 1960. A manual of sea water analysis. Bulletin of the Fisheries Research Board of Canada, no. 125, 185 pp.

——— 1965. A manual of sea water analysis. Bulletin of the Fisheries Research Board of Canada, no. 125, 203 pp.

TALLING, J. F. 1957. Photosynthetic characteristics of some fresh-water plankton diatoms in relation to underwater radiation. New Phytologist, vol. 56, pp. 29–50.

TAYLOR, W. R., and J. D. PALMER. 1963. The relation between light and photosynthesis in intertidal benthic diatoms. Biological Bulletin, vol. 125, p. 395.

TRUESDALE, G. A., A. L. DOWNING, and G. F. LOWDEN. 1955. The solubility of oxygen in pure water and sea water. Journal of Applied Chemistry, vol. 5, pp. 53–62.

WHITFORD, L. A. 1960. The current effect and growth of fresh-water algae. Transactions of the American Microscopical Society, vol. 79, pp. 302–309.

WHITFORD, L. A., and G. J. SCHUMACHER. 1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. Ecology, vol. 45, no. 1, pp. 168–170.

ZOBELL, C. E., and C. B. FELTHAM. 1942. The bacterial flora of a marine mud flat as an ecological factor. Ecology, vol. 23, pp. 69–78.